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Occurrence of *Epistylis anastatica* (Linnaeus, 1767) (Ciliophora: Peritrichia) on *Mesocyclops isabellae* Dussart & Fernando (Crustacea: Copepoda: Cyclopoida) in India, with an annotated checklist of species of *Epistylis* reported as Epibionts of Cyclopoid Copepods and resources for their identification

JOHN C. CLAMP[1,4], TAPAS CHATTERJEE[2] & GREGORIO FERNANDEZ-LEBORANS[3]

[1]*Department of Biology, North Carolina Central University, Durham 27707 U.S.A. E-mail: jclamp@nccu.edu*
[2]*Department of Biology, Indian School of Learning, I.S.M. Annexe, P.O. – I. S. M., Dhanbad 826004, Jharkhand, India. E-mail: drtchatterjee@yahoo.co.in*
[3]*Department of Zoology, Faculty of Biology, Pnta 9, Complutense University, 28040 Madrid, Spain. E-mail: greg@bio.ucm.es*
[4]*Corresponding author*

Abstract

The colonial peritrich ciliate *Epistylis anastatica* (Linnaeus, 1767) was discovered living as an epibiont on *Mesocyclops isabellae* Dussart & Fernando, 1988 collected from a pond in Andhra Pradesh state, India. This is the first report of *Epistylis* on this host, and a description of its morphological characteristics is provided. The biomass of colonies of *E. anastatica* relative to that of their hosts was relatively high, being greater than that of the host in some cases (8.11 mm^3 vs. 1.14 mm^3 or less), and this epibiotic burden has the potential to have an impact on the host's activities. Relationships between epibiotic peritrichs and microcrustaceans like cyclopoid copepods may be much more complex than previously supposed and merit more thorough investigation. Species of *Epistylis* are commonly found on cyclopoid copepods, but resources for taxonomic identification are limited and scattered; therefore, an annotated checklist of all species reported from cyclopoid copepods and a summary of the diagnostic characteristics of each one is provided as an aid to investigators. Some records of *Epistylis* spp. from cyclopoid copepods that are accompanied by documentary evidence are misidentifications, raising the suspicion that many other undocumented records also may be erroneous; therefore, it is suggested that authors provide supplementary descriptions and figures.

Key words: peritrich ciliate, freshwater plankton, biogeography, taxonomy, predator-prey relationship

Introduction

Many species of peritrich ciliates, most of which attach to solid substrates, are known to live as epibionts on a wide variety of crustaceans (Kahl, 1935; Sprague & Couch, 1971; Fernandez-Leborans & Tato-Porto, 2000). This includes species of the genus *Epistylis*[1] Ehrenberg, 1830, which is characterized by formation of colonies of zooids supported on a non-contractile stalk and possession of a peristomial lip that folds outward when the oral area (peristome) is expanded ("epistyliform" peristome). In particular, there are many records of species of *Epistylis* attached to the exoskeletons of freshwater cyclopoid copepods (Kahl, 1935; Foissner *et al.*, 1999), a group of microcrustaceans that constitute a significant part of planktonic communities in a variety of freshwater habitats (Thorp & Covich, 2010) and, thus, have been studied intensively by ecologists and taxonomists.

In the present study, colonies of a species of *Epistylis* were discovered on a sample of the cyclopoid copepod *Mesocyclops isabellae* Dussart & Fernando, 1988 from the Guntur district of Andhra Pradesh, India and identified as *E. anastatica* (Linnaeus, 1767). This is first report of a member of *Epistylis* as an epibiont on this host. In the process of identifying the epibionts on *M. isabellae*, we were impressed by the difficulty created by scattered,

1. Recent molecular investigations (Miao *et al.*, 2004; Utz *et al.*, 2010) have revealed that *Epistylis* and the family Epistylididae are paraphyletic taxa; however, the morphological definition of *Epistylis* given by Ehrenberg (1838) remains in use, pending completion of a formal taxonomic revision of the genus and family.

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inconsistent taxonomic descriptions and faunistic records. Accordingly, we also present an annotated list of species of *Epistylis* that have been reported as epibionts of cyclopoid copepods and a summary of their diagnostic characteristics that will be a resource for investigators who encounter these peritrichs and wish to identify them more reliably.

Materials and methods

Specimens of *M. isabellae* with attached colonies of a species of *Epistylis* were collected on October 2, 2012 by Dr. Y. Ranga Reddy (Acharya Nagarjuna University, Andhra Pradesh, India) with a plankton net from a rain-fed, shallow pond near the entrance of the Guthikonda Caves, which are located in southeastern India ~ 8 km southwest of the town of Piduguralla in the Palnadu area of the Guntur district of Andhra Pradesh state. This locality is in the Eastern Ghats ecoregion, lying at the northern end of the Nallamalla Hills, near the transition to the coastal plain of Andhra Pradesh. The pond is ~ 0.5 ha in area and < 2 m deep, with unidentified macro-algae and some emergent macrophytes (e.g., *Eichhornia* sp.) along the margins. There were no visible masses of decaying vegetation, but the bottom was muddy and, therefore, could have consisted at least partly of decomposed organic matter. Hołyńska *et al.* (2003) was used to identify the copepod host.

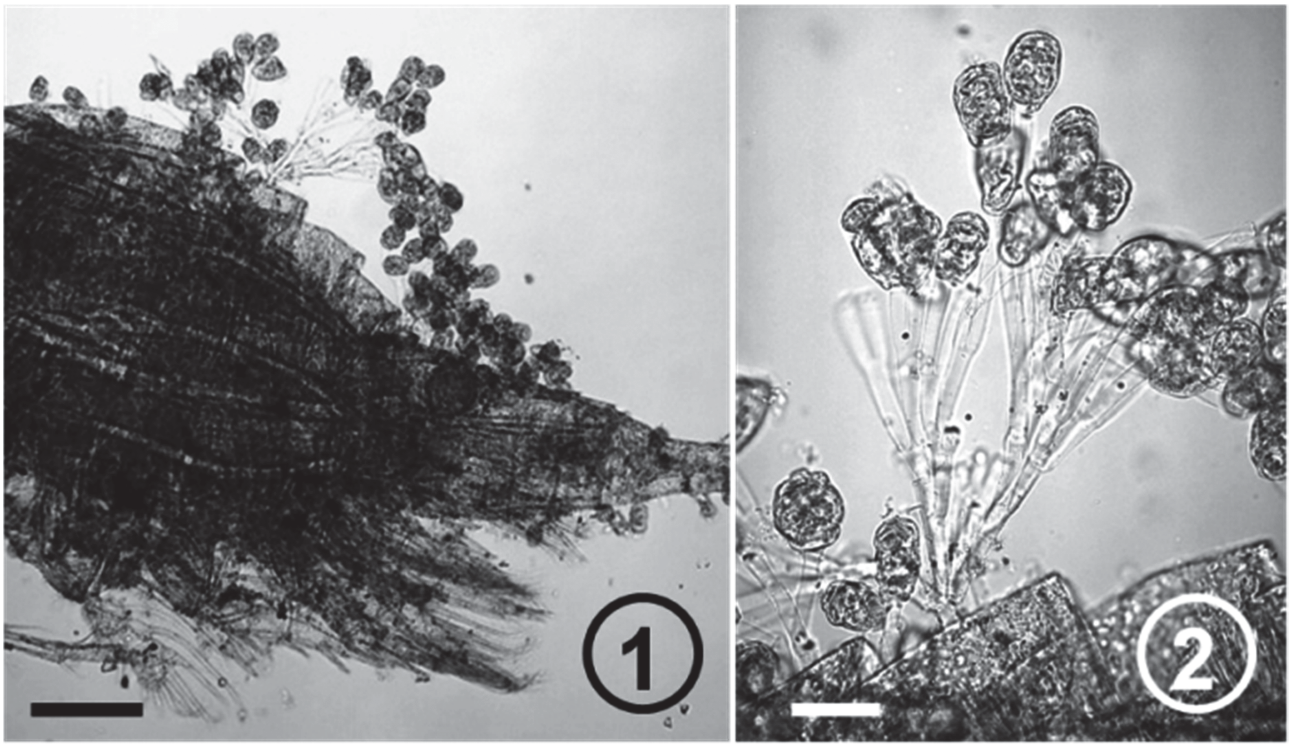
Copepods were preserved in 70% ethanol for taxonomic studies, and organisms hosting colonies of peritrichs were isolated from samples using a binocular microscope. The ciliates were observed with a Zeiss compound microscope equipped with an Image Analysis (Zeiss K 300) system and an Olympus BX40 microscope. Measurements of ciliates were performed with the computer program ScopePhoto 2.0. Biomass of colonies was estimated by determining cell volumes of zooids from measurements, and biomass of hosts was estimated from measurements of copepods. To aid in identification, colonies of peritrichs also were isolated and stained with methyl green and neutral red.

Results

Description of *Epistylis anastatica* on *M. isabellae* (Figures 1–9; Table 1**)**. Colonial, with relatively tall colonies composed of many (from 25–30 up to more than 240) zooids. Stalk lacking spasmoneme and rigid, branching pattern of stalk symmetrically dichotomous to irregular. Primary stalk of colony short to moderately long, measuring 80–256 µm long, with diameter of 14–18 µm (n = 4; not reported in Table 1). Individual 2º and 3º stalks of zooids 75.2–178.6 µm long, with diameter of 7.5–13.2 µm. Contracted zooids ovoid to subcylindrical, 33.2–50.8 µm long x 26.3–33.9 µm wide. Edge of peristomial lip constricted to form projecting tube sometimes described as “schnauzenformigen” (snout-like). Scopula of contracted zooids retracted within body to moderate degree, encircled by at least one distinct fold; additional folds encircling aboral end of some contracted zooids. Macronucleus of fixed cells elongate, cylindroid, C-shaped, longitudinally oriented, measuring 43.2–56.4 µm x 3.8–7.5 µm. Spherical micronucleus with diameter of 3.8–7.6 µm located near macronucleus. Infraciliature not observed. Surface of body with visible, transverse pellicular striations.

TABLE 1. Morphometry of fixed specimens of *Epistylis anastatica* observed in the present study (n = 60). Measurements expressed in µm (SD = Standard Deviation).

Character	Mean	SD	Range
length of body	43.9	± 4.8	33.2–50.8
width of body	29.5	± 2.1	26.3–33.9
length of macronucleus	49.6	± 3.6	43.2–56.4
width of macronucleus	5.8	± 1.0	3.8–7.5
length of stalk	142.3	± 30.1	75.2–178.6
width of stalk	9.3	± 1.9	7.5–13.2
width of peristomial disc	12.6	± 1.4	10.8–15.2
number of pellicular striations	68.3	± 4.5	62–75



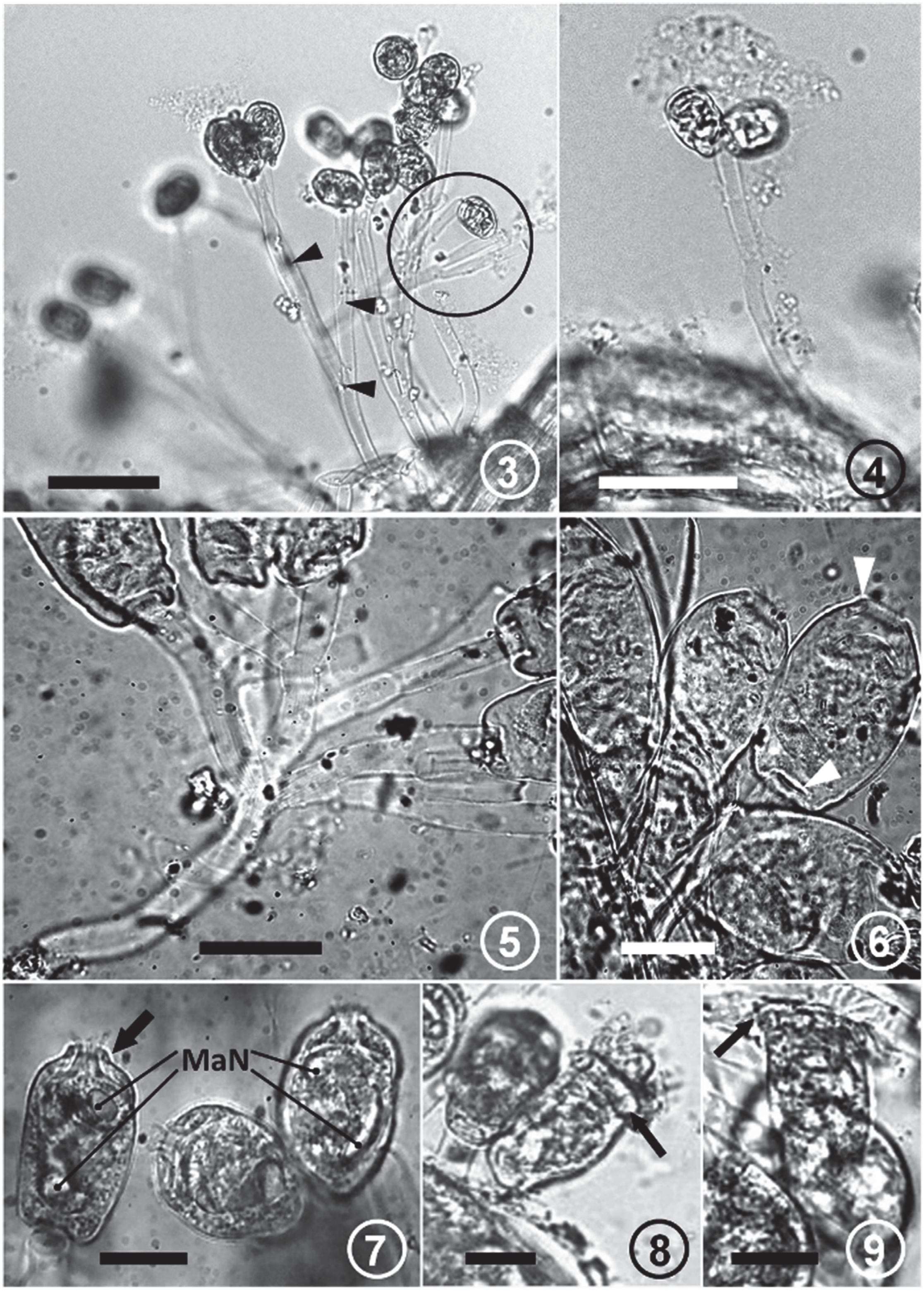
FIGURES 1–2. Colonies of *Epistylis anastatica* attached to the metasome and urosome of *Mesocyclops isabellae.* Scale bar = 250 µm in 1 and 50 µm in 2.

Occurrence of *E. anastatica* on the body of *M. isabellae* and biomass of epibionts relative to the biomass of hosts. Colonies of *E. anastatica* were observed on all three major divisions of the bodies of copepod hosts. They were attached only to the dorsal surfaces of the cephalosome and metasome but were attached to all sides of the urosome. There were no other species of *Epistylis* or other genera of peritrichs attached to the copepods. Of many individuals of *M. isabellae* in the original sample, relatively few were infested with *E. anastatica* (exact accounts not available from the collectors). Calanoid copepods (*Neodiaptomus lindbergi* Brehm, 1951–abundant; *Heliodiaptomus viduus* [Gurney, 1916]–scarce) also were present in the sample, but none were infested with ciliates. The sample also contained ostracods, naupliar and copepodite stages of copepods, rotifers, tadpoles, and water mites, none of which hosted *E. anastatica*.

In some cases, a significant biomass of epibionts was observed on individuals of *M. isabellae*. On several copepods, the biomass of epibionts was higher than that of the host. The greatest number of zooids observed on a single host was 242 per copepod, which constitutes a biomass of 8.11 mm^3. None of the copepods had a biomass greater than 1.14 mm^3 (Reddy, pers. comm.).

Discussion

Taxonomic identification of *E. anastatica* on *M. isabellae*. The fixed colonies of peritrichs with contracted zooids observed on *M. isabellae* fit authoritative published descriptions of *E. anastatica* (Ehrenberg, 1838; Foissner *et al.*, 1992, 1999) well enough to allow them to be identified with confidence even though living zooids were not available. With a few notable exceptions (e.g., family Lagenophryidae), living individuals are necessary to make definitive morphological identifications of peritrichs. This is because some of the most critical diagnostic characteristics (e.g., width of the peristome relative to the body, thickness and appearance of the peristomial lip) are features of the fully expanded oral area. Ideally, the infraciliature of the oral region, particularly the infundibular polykineties, and the pellicular striae (series of raised ridges that encircle the body) also should be examined in cells stained by means of the protargol (Foissner, 1992a) and dry silver nitrate (Foissner, 1992b) methods. Unfortunately, characteristics of the infraciliature and pellicular striae could not be observed in the present material



FIGURES 3–9. *Epistylis anastatica* attached to the exoskeleton of *Mesocyclops isabellae*. 3–5: views of the stalk, showing the dichotomous branching pattern and long primary stalk; arrowheads in fig. 3 indicate the branching points in an asymmetrically dichotomous colony and to its right are the abandoned stalks of a symmetrically dichotomous colony (region encircled); 4, immature colony; note the elongate primary stalk; 5, stalks of two symmetrically dichotomous colonies (one is lying over the other, which is slightly out of focus). 6–9: characteristics of zooids; 6, the upper arrowhead indicates the edge of the peristomial lip, and the lower arrowhead indicates the scopula (circular, aboral region that secretes the stalk and attaches the zooid to it); 7, arrow indicates the projecting tube formed by constriction of the peristomial lip when cell contracts ("schnauzenformigen"); MaN, longitudinally oriented macronucleus; 8–9, zooids that remained expanded when fixed; arrow indicates the peristomial lip in both figures. Scale bar = 100 µm in 3–4 and 25 µm in 5–9.

and, in any event, have not been described for most species of *Epistylis*, leaving features of gross morphology as the primary characteristics available for making taxonomic identifications until authoritative redescriptions of species are published.

The following combination of characteristics support the identification of the colonial peritrichs discovered on *M. isabellae* as *E. anastatica*: tall colonies (Fig. 1) with a rigid stalk lacking a spasmoneme (Fig. 2–4), mostly symmetrical dichotomous branching (Fig. 1–5, 10), mature colonies with many (25–240) zooids (Fig. 1), peristomial lip constricted into a projecting tube (Fig. 7), and an elongate macronucleus that is oriented longitudinally relative to the main axis of the cell (Fig. 7). Although we were not able to examine living ciliates, a few zooids in the sample had remained expanded when fixed. This allowed us to determine that the width of the peristome is approximately the same as the width of the cell (Fig. 8–9) and that the peristomial lip is relatively thin (Fig. 8–9), both of which are diagnostic characteristics of *E. anastatica* (Table 2).

TABLE 2. Diagnostic characteristics of species of *Epistylis* recorded from cyclopoid copepods. The table can be used as an informal key to narrow down the possibilities for identification of species if one moves from left to right. A traditional, dichotomous key is not provided because variability in form of some species makes it difficult to provide unambiguous choices in all cases. Samples that contain colonies at different stages of development are best for identification because branching pattern is easier to determine in such a series. To verify identifications, it is best to consult the original descriptions of species and, if available, recent sources that provide careful documentation of morphological characteristics (e.g., Foissner *et al.*, 1999).

Species	**CoSz**[a]	**CoSh**[b]	**BrP**[c]	**ZoS**[d]	**PW**[e]	**PLT**[f]	**MaN**[g]	**Dsct**[h]	**Host**[i]
E. breviramosa	S	Cl	Umb	El, Cydr	W	Tck	Lng	none	Cycl
E. caldwelli	S	Cl	Irg	El, Ovd	N	Tck	Lng	TB	Cycl
E. invaginata	S	Cl	AD	Sph	W	Tn	Lng	none	Cycl
E. magna	S	Cl	Irg	Sbcn	N	Tck	Trn	LF, MCF, Prjt	Lern
E. pygmaeum	S	Cl	SD or Irg	Sph or Ovd or Sbcn	N	Tck	Lng	none	Cycl
E. umbellina	S	Cl	Umb	——[j]	——	——	——	none	Cycl
E. umbilicata	S	Arb	AltS	Sl, Pyrf	N	Tn	——	none	Cycl
E. zschokkei	S	Cl	Irg	Ovd	N	Tck	Trn	OEI, SB	Cycl
E. anastatica	T	Arb or Cun	AltS to Irg	El, Sl, Sbcn to Sbcy	N	Tn	Lng	SerB, Prjt	Cycl
E. branchiophila[k]	T	Arb	Pin	Sph	——	——	——	none	Lern
E. cyprinacea	T	Arb	AltS	Ovd to Cydr	W	Tn	Trn	Bf, MaMi, Prjt	Lern
E. digitalis	T	Arb	AltI	El, Sl, Cydr, TaSc	W	Tck	Lng	RB	Cycl
E. epibarnimiana	T	Arb	Irg	Ovd	N	Tck	Trn	none	Lern
E. niagarae[k]	T	Arb	AltI	El, Sl, Cnst	W	Tn	Trn	Prjt	Cycl
E. plicatilis	T	Arb or Cun	AltI,	El, Sbcn, TaSc, TF	W	Tck	Trn	AbFd, LB	Cycl

[a]size of colony; abbreviations: S, short, with few zooids; T, tall, with many zooids. Note: measurements of colonies are not given because their size can vary according to their degree of development and the host to which they attach; as a general rule, colonies can be considered short if they are less than 400–500 µm tall at maturity and tall if they are greater than this (up to 3000–4000 µm in height).

[b]shape of colony; abbreviations: Arb, arborescent; Cl, simple cluster of zooids; Cun, cuneate

[c]branching pattern of colony; abbreviations (basic pattern of branching): AltI, alternating and irregular; AltS, symmetrically alternating; AD, asymmetrically dichotomous; Irg, irregular (no discernible pattern); Pin, pinnate with approximately opposite branches; SD, symmetrically dichotomous; Umb, umbellate.

[d]shape of zooid; abbreviations: Cnst, constricted aboral of peristome and widest at midpoint; Cydr, cylindroid; El, elongate; Ovd, ovoid, Pyrf, pyriform (tapering toward peristome); Sbcn, subconical; Sl, slender; Sph, spheroid; Sbcy,

subcylindroid; TaSc, tapering toward scopula; TF, contracted zooid with transverse folds at regular intervals around body.

[e]diameter of peristome relative to width of zooid's body; abbreviations: W, diameter of peristome approximately equal to or slightly greater than maximum width of body; N, diameter of peristome slightly to moderately less than maximum width of body.

[f]relative thickness of peristomial lip; abbreviations: Tck, relatively thick (prominent lip); Tn, relatively thin (inconspicuous lip).

[g]orientation of macronucleus; abbreviations: Lng, cyclindroid macronucleus oriented parallel to long axis of zooid's body; Trn, cyclindroid macronucleus oriented transversely to long axis of body (typically curved into "C" shape).

[h]Distinctive characteristics; abbreviations: AbFd, aboral half of cell folding to form series of several folds when contracted; Bf, two robust 2º branches ramify to give the colony a bifurcate organization; LB, primary stalk and secondary branches often elongate; MaMi, zooids in two distinct size classes (microzooids vs. macrozooids); MCF, peristomial lip with medial circumferential infolding that appears to divide it into two sections; OEI, edge of peristomial lip indistinct and poorly visible when expanded; Prjt, peristomial lip constricts to form projecting tube ("snout") when contracted; RB, stalks encircled by closely spaced ridges; SB, extremely short branches; SerB, often with series of terminal branches from single 2º or 3º branch; TB, extremely thick, robust branches with same diameter as zooids.

[i]taxonomic group of copepod host; abbreviations: Cycl, family Cyclopidae; Lern, Lernaeidae.

[j]characteristic not described

[k]records of this species on cyclopoid hosts are misidentifications (see comments in annotated list), but it is included here for purposes of comparison.

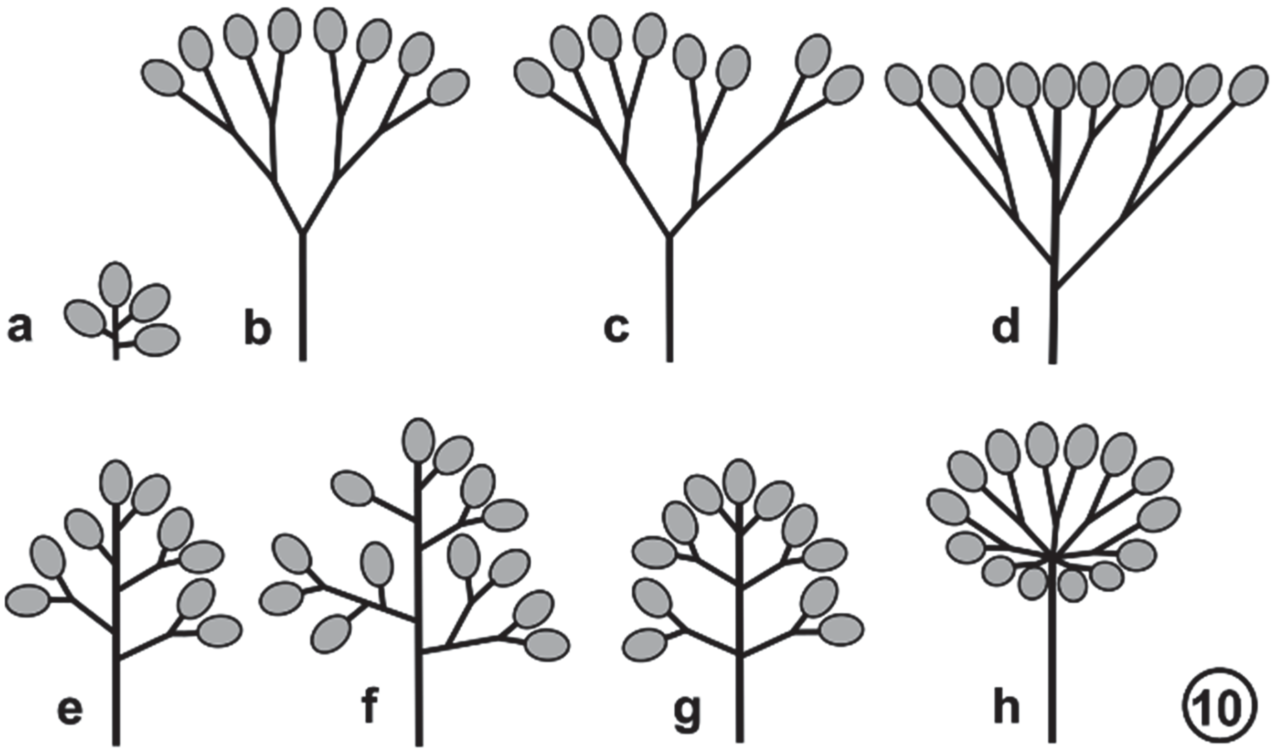


FIGURE 10. Diagrams that illustrate the possible forms and branching patterns of colonies of *Epistylis* spp. given in Table 2. Colony forms: a, simple cluster; b–c, e–h, arborescent; d, cuneate (wedge-shaped, with all stalks terminating at the same level); branching patterns: a, irregular (no discernible pattern); b–d, symmetrically dichotomous; c, asymmetrically dichotomous; e symmetrically alternating; f, asymmetrically alternating; g, pinnate; h, umbellate. Notes: colonies such as 'b' and 'c' are sometimes described as fan-shaped (flabellate); cuneate colonies (d) are sometimes incorrectly described as umbellate, a term that can be used properly only to describe a pattern in which all of the 2º branches radiate in different planes from a single point (compare 'd' and 'h' to see the difference); pinnate colonies like those illustrated in 'g' are an extreme variant of the alternating pattern in which pairs of 2º branches arise from points so close together that they seem to be opposite one another.

Comments on the biomass of *Epistylis* sp. relative to that of *M. isabellae*: relationships between epibionts and their copepod hosts. Overall, epibiosis of algae, protists, or rotifers on small planktonic animals is thought to have negative consequences for the fitness of their hosts. High densities of epibionts may constitute a considerable

physical burden for planktonic microcrustaceans, interfering with vital activities such as locomotion, predator-avoidance, and feeding (Herman & Mihursky, 1964; Kankaala & Eloranta, 1987; Willey *et al.*, 1990; Willey & Threlkeld, 1993; Barea-Arco *et al.*, 2001; Regali-Seleghim & Godinho, 2004; Bickel *et al.*, 2012; Burris & Dam, 2014).

In the present study, the most heavily infested individuals of *M. isabellae* were carrying a population of *E. anastatica* with several times the biomass of the host. This certainly had the potential to exert a markedly negative effect on the locomotion of the copepods. In general, larger species of free-living cyclopoid copepods >1.4 mm (e.g., species of *Cyclops* O.F.Müller, 1785, *Macrocylops* Claus, 1893, *Megacyclops* Kiefer, 1927, *Mesocyclops* G.O.Sars, 1914) are either exclusively raptorial predators of a wide variety of protists and small animals or feed mostly on algae (e.g., some species of *Eucyclops* Claus, 1893) while capturing few, if any, prey (Fryer, 1957; Anderson, 1970; Marten & Reid, 2007). It might be expected, therefore, that nutritional differences between species of freshwater cyclopoids would translate into differences in the way that they are affected by heavy infestations of epibiotic peritrich ciliates. For instance, raptorial cyclopoids might find both their ability to seize prey and escape their own predators impeded by the presence of epibiotic ciliates, but epibionts would not be expected to interfere with feeding in hosts that obtain most of their nutrition by grazing on algae.

Freshwater cyclopoid copepods are major components of the food webs of their communities (Thorp & Covich, 2010); thus, the lack of attention given to epibionts in investigations into the ecology of cyclopoids is surprising. Papers that investigate relationships between epibiotic species of *Epistylis* and zooplankton in fresh water have focused almost exclusively on *Daphnia* O.F. Müller, 1785 and other cladocerans (Xu, 1993), calanoid copepods (Xie *et al.*, 2001; Xu & Burns, 1991), or suspension-feeding rotifers (Gilbert & Schröder, 2003), all of which have nutritional lifestyles that are markedly different from large cyclopoids.

One specific trophic role of cyclopoids in freshwater ecosystems that could be affected by the presence of epibiotic *Epistylis* spp. is their ability to prey successfully on mosquito larvae. Some of the larger cyclopoids, including ones that are recorded as hosts of *Epistylis* spp. (Table 3) are well-known predators of first- and second-stage mosquito larvae, and there is an extensive literature on the use of such cyclopoids (mainly *Mesocyclops* spp.) for biological control of mosquito populations (Marten & Reid, 2007). In general, aquatic predators such as cyclopoids rely on a complex series of mechanisms, both sensory and locomotory, to detect prey organisms and overcome their ability to elude capture by executing evasive movements (Kerfoot, 1978; Andrade & López, 2005). The effect of epibiotic ciliates on the mechanisms for detection and capture of prey by cyclopoids has not been investigated. This should be viewed as a possible factor in the effectiveness of cyclopoids for control of mosquito larvae, especially in bacteria-rich environments conducive to growth of epibiotic peritrichs. Furthermore, some epibiotic species of *Epistylis* use both cyclopoids and mosquito larvae as hosts (Laird, 1960), creating the possibility that the epibionts might act as a common factor in the predator-prey relationships of a host-complex.

Another significant role that cyclopoid copepods play in aquatic food webs is as prey for larger fish larvae and predators of smaller fish larvae (Fryer, 1957; Anderson, 1970). Again, this raises the question of the type and complexity of impacts on food webs that might result from the presence of heavy populations of epibiotic ciliates on the copepods.

All epibiotic peritrichs are suspension feeders on bacteria and other small organisms and appear to benefit mainly from receiving particulate food carried to them in water currents generated by locomotion or respiratory movements of the host (Clamp, 1973); therefore, it is difficult to form any hypotheses about how differences in the lifestyles of cyclopoid copepods serving as hosts might affect the feeding activities of their epibionts. However, heavy loads of epibiotic peritrichs that form large colonies (e.g., *Epistylis*, *Zoothamnium* Bory de St. Vincent, 1820, *Carchesium* Ehrenberg, 1831) might have a self-limiting effect by reducing the force of water currents produced by the host or creating competition for particles between zooids in tightly packed colonies. This type of effect would operate differently upon an epibiotic population of *Epistylis* or *Carchesium* than on a population of epibiotic *Zoothamnium* because the latter is a syncytium, with all zooids linked by the cytoplasm that contains the spasmoneme of the stalk. Theoretically, zooids in a colony of *Zoothamnium* should be able to share absorbed food (this has not been confirmed experimentally, however), but individual zooids in a colony of *Epistylis* are isolated on a rigid stalk with no cytoplasmic component and, thus, must certainly feed themselves.

Most of the attention paid to the relationships between epibionts and microcrustaceans has focused either on deleterious effects upon the host or benefits to the epibiont. One area that has been neglected is the possible benefits of heavy infestations of epibionts to particle-feeding or grazing hosts (i.e., ones whose feeding might not

be impacted negatively by the presence of epibionts). The ability of cyclopoids to capture specific types of prey is known to be affected by species-specific characteristics of prey organisms, including shape, size, and hardness/softness of the body (Li & Li, 1979). It is possible that a dense covering of peritrich ciliates might "camouflage" common prey items of cyclopoids (e.g., cladocerans) or make them more difficult to seize. In turn, dense infestations of peritrichs on the cyclopoids might give them some measure of protection against predators such as larval fish or predatory insect larvae. Heavy infestations of epibiotic peritrichs do seem to be correlated with downturns in the host populations of calanoid copepods and cladocerans (Herman & Mihursky, 1964; Willey & Threlkeld, 1993); however, it should not be automatically assumed that an association is always uniformly negative for the host. Indeed, Barea-Arco *et al.* (2001) found that positive and negative effects from an association between a cladoceran and a green microalga offset one another to result in the association having a neutral effect on survival of the host. There may be many such neutral relationships between planktonic microcrustaceans and peritrich ciliates.

TABLE 3. Occurrences of species of *Epistylis* as epibionts on cyclopoid copepods.

Hosts[a]	Species of *Epistylis*[b]											Total records
	ast	cwl	cyp	dtl	epb	mag	plt	pgm	umb	zhk	spc	
Acanthocyclops robustus											+	1
A. vernalis[c]				+			+	+		+		4
Cyclops quadricornis				+				+				2
C. strenuus	+						+	+		+		4
C. vicinus											+	1
Diacyclops bicuspidatus				+			+	+			+	4
D. bisetosus				+								1
Eucyclops agilis	+			+			+					3
E. macruroides											+	1
E. serratulus	+			+			+	+		+	+	6
E. speratus											+	1
Lernaea cyprinacea			+			+					+	3
L. barnimiana					+							1
Macrocyclops albidus[c]	+							+	+			3
M. fuscus[c]	+			+				+	+	+		5
Megacyclops viridis[c]	+			+				+		+	+	5
Mesocyclops brasilianus											+	1
M. isabellae											+	1
M. leuckarti	+	+					+	+			+	5
Paracyclops fimbriatus	+									+	+	3
Thermocyclops decipiens											+	1
Tropocyclops extensus								+				1
Total	8	1	1	8	1	1	6	10	2	6	13	57

[a]Eighteen records on unidentified hosts (e.g., *Cyclops* sp.) have been omitted from the table. These are the following: 6 from *E. anastatica*; 5 from *E. pygmaeum*; 2 each from *E. digitalis* and *E. plicatilis*; 1 each from *E. breviramosa*, *E. invaginata*, and *E. umbellina*.

[b]Abbreviations: ast, *E. anastatica*; cwl; *E. caldwelli*; cyp, *E. cyprinaceae*; dtl, *E.digitalis*; epb, *E. epibarnimiana*; mag, *E. magna*; plt, *E. plicatilis*; pgm, *E. pygmaeum*; umb, *E., umbilicata*; zhk, *E. zschokkei*; spc, unidentified species of *Epistylis*.

[c]Species utilized for control of mosquito larvae (Marten & Reid, 2007).

Aids to identifying species of *Epistylis* reported as epibionts of cyclopoid copepods: currently available resources, summary of diagnostic characteristics, and annotated checklist. There are currently 34 accepted families in the order Cyclopoida (Walter & Boxshall, 2014). Epizoic species of *Epistylis* have been reported from hosts in only two of these, the family Cyclopidae Rafinesque, 1815 (free-living) and the family Lernaeidae Cobbold, 1879 (ectoparasitic). These will be treated separately in the list.

In most literature sources, hosts in the Cyclopidae have been cited as species of *Cyclops* O.F.Müller, 1785; we have listed them under their current generic assignments. The resource that we used for determining the accepted names of cyclopoid hosts was the *World of Copepods* on-line database (Walter & Boxshall, 2014). Users also should be aware that some records of associations with unidentified species of *Cyclops* in the list below are likely to have been species that have been assigned to other genera since their records were published. Useful resources for taxonomic identification of cyclopoid copepods are Hudson & Lesko (2003) and Haney (2013).

The monographs by Foissner *et al.* (1992, 1999) are the best sources for descriptions and figures of *E. anastatica* (and its synonyms *E. lacustris* and *E. nympharum*), *E. digitalis*, *E. pygmaeum*, and *E. plicatilis*. Kent (1881) and Keiser (1921) are somewhat outdated in terms of nomenclature but both contain useful descriptions of epibiotic species of *Epistylis*. Likewise, Kahl (1935) remains a useful general reference with short descriptions of most of the species in the list as well as information on substrates and reproductions of figures from the literature. The following papers are useful for individual species: Claparède and Lachmann (1858) for *E. invaginata* and *E. umbilicata*; Stiller (1931) for *E. breviramosa* and *E. pygmaeum* (as *E. ovum*, one its synonyms); Laird (1960) for *E. caldwelli*; Kellicott (1883), Matthes & Guhl (1973), and Matthes (1974) for *E. niagarae*; Van As and Viljoen (1984) for *E. cyprinacea*, *E. epibarnimiana*, and *E. magna*.

Species of *Epistylis* can be identified by means of morphological characteristics of the colony (i.e., size, number of zooids, branching pattern of the stalks) and zooids (shape, width of the peristome, thickness of the peristomial lip, shape and orientation of the macronucleus). Table 2 and Fig. 10 present a summary of these diagnostic characteristics for the species of *Epistylis* recorded as epibionts of cyclopoid copepods as an aid to identification.

The genus *Epistylis* presently contains ~185 known morphospecies (Roberts, 2014), many of which are "poorly known" (i.e., represented in the literature only by the original taxonomic description, which is often short or incomplete—a good example from the list below is *E. umbellina* Fauré-Frémiet, 1905). Therefore, investigators should be aware that there is an excellent chance that they may encounter a species of *Epistylis* that is not covered in the present paper. Unfortunately, no single, comprehensive, up-to-date reference exists for taxonomic identification of species of *Epistylis*, and investigators who wish to identify a species that does not match the description of any of those known to occur on cyclopoid copepods will, by necessity, be forced to begin with Kahl (1935) and search the literature for descriptions of new species discovered since publication of that monograph.

Some of the species of *Epistylis* that are known to occur on cyclopoid copepods are in need of taxonomic redescription. Few have been stained with protargol and silver nitrate to reveal the taxonomically significant characteristics of the oral infraciliature and silverline system (Lom, 1964; Foissner *et al.*, 1992, 1999). Likewise, only one species recorded as an epibiont of cyclopoids, *E. plicatilis*, has been included in molecular investigations (Miao *et al.*, 2001; Utz *et al.*, 2010).

Species of *Epistylis* that have been reported on free-living, planktonic, cyclopid copepods (Table 3) can be categorized on the basis of gross morphology as those that form relatively small, short colonies versus those that form relatively large, tall colonies (Table 2). The following species fall into the first category:

- ***Epistylis breviramosa*** **Stiller, 1931; records on substrates other than cyclopoid copepods:** *Daphnia* sp. (type host); **record on cyclopid:** *Cyclops* sp., Czechoslovakia (Šrámek-Hušek, 1948); *Cyclops* sp., Slovakia (Stloukal, 1999).
- ***Epistylis caldwelli*** **Laird, 1960; records on substrates other than cyclopoid copepods:** two species of mosquito larvae, a corixid, exuviae of dragonfly larvae; **record on cyclopid:** Singapore, *Mesocyclops leuckarti* (Claus, 1857).
- ***Epistylis invaginata*** **Claparède and Lachmann, 1858; records on substrates other than cyclopoid copepods:** hydrophilid beetle (type host); **record on cyclopid:** *Cyclops* sp., Germany (Sommer, 1951).
- ***Epistylis pygmaeum***[2] **(Ehrenberg, 1838); records on substrates other than cyclopoid copepods:** cladocerans, ostracods, rotifers, mayfly larvae, aquatic plants (see Foissner *et al.*, 1999 for sources of records);

records on cyclopids (as *Carchesium pygmaeum*): *Cyclops* sp., Germany (Ehrenberg, 1838); (**as *Scyphidia pyriformis***): *Cyclops quadricornis* (Linnaeus, 1758), Switzerland (Perty, 1852); **(as *Rhabdostyla ovum*** Kent, 1882**):** *Cyclops* sp., Estonia (Schneider, 1909); *Acanthocyclops vernalis* (Fischer, 1853), *C. strenuus* Fischer, 1851*, Diacyclops bisetosus* (Rehberg, 1880), *Eucyclops serratulus* (Fischer, 1851)*, Macrocyclops albidus* (Jurine, 1820)*, M. fuscus* (Jurine, 1820)*, Megacyclops viridis* (Jurine, 1820)*, Mesocyclops leuckarti*, Switzerland (Keiser, 1921); *Cyclops* sp., China (Wang & Nie, 1933); **(as *Epistylis ovum*** [Kent, 1882]**):** *Cyclops* sp., Hungary (Stiller, 1931, 1942); (**as *Epistylis pygmaeum***): *Cyclops* sp., Austria (Foissner *et al.*, 1999); *Tropocyclops extensus* Kiefer, 1931, experimental conditions in laboratory culture (Gilbert & Schröder, 2003). Comments: This species is not only found on a variety of substrates but is also somewhat variable in form and in the degree to which the colonies develop (see figures in Foissner *et al.*, 1999 for examples). Therefore, it is no surprise that it has been known under several names (Foissner *et al.*, 1999). The intraspecific variability of the species ordinarily would cast doubt on many of the records, especially those not accompanied by a figure or detailed description; however, the confirmation of its lack of host-specificity by Gilbert & Schröder (2003) supports a hypothesis that this widespread species (reliably reported only from Europe and Asia) develops slightly different morphologies on different hosts and substrates.

- ***Epistylis umbellina*** **Faur-Fremiet, 1906; records on substrates other than cyclopoid copepods:** none; **record on cyclopid:** *Cyclops* sp., France (type host).
- ***Epistylis umbilicata*** **Claparède & Lachmann, 1858; records on substrates other than cyclopoid copepods:** mosquito larvae (type host); freshwater oligochaete annelids, Switzerland (Keiser, 1921); **records on cyclopids:** *Macrocyclops albidus, M. fuscus*, Switzerland (Keiser, 1921).
- ***Epistylis zschokkei*** **(Keiser, 1921); records on substrates other than cyclopoid copepods:** *Canthocamptus* spp. (harpacticoid copepods), Switzerland (Keiser, 1921); **records on cyclopids:** *Acanthocyclops vernalis*, *Cyclops strenuus, Eucyclops serratulus, Macrocyclops fuscus, Megacyclops viridis*, *Paracyclops fimbriatus* (Fischer, 1853), Switzerland (Keiser, 1921); *M. fuscus*, Germany (Nenninger, 1948); *A. vernalis*, *M. fuscus*, Slovakia (Stloukal, 1999). Comments: This species was placed originally in the genus *Opercularia* Goldfuss, 1820 by Keiser (1921) because its peristome appeared to him to be the specialized type that is typical of operculariids, which have a peristomial lip that does not fold outward when the zooid expands.
- ***Epistylis*** **sp. (in Bozkurt & Genc, 2009); records on substrates other than cyclopoid copepods**: cladocerans (6 spp.), rotifers (2 spp.); **Records on cyclopids:** *Acanthocyclops robustus* (G.O.Sars, 1863), *Cyclops vicinus* Ulyanin, 1875, *Diacyclops bicuspidatus* (Claus, 1857), *Eucyclops macruroides* (Lilljeborg, 1901), *E. speratus* (Lilljeborg, 1901), *Megacyclops viridis*, *Mesocyclops leuckarti*, *Paracyclops fimbriatus*. Comments: This set of records resulted from an ecological investigation of epibiotic populations of an unidentified species of *Epistylis* in the Asi River, in the extreme south-central part of Turkey. It is included here because figures in Bozkurt & Genc (2009) depict a species with obviously short colonies. Unfortunately, the authors provided no description that might make it possible to identify their species. However, its occurrence on a variety of hosts and the general appearance of the colonies strongly suggest that it might have been *E. pygmaeum*. It is also possible, of course, that this set of records may represent more than one species of *Epistylis*.
- ***Epistylis*** **sp. (in López *et al.* 1998); records on substrates other than cyclopoid copepods:** cladocerans (3 spp.), *Notodiaptomus maracaibensis* Kiefer, 1954 (calanoid copepod); **Records on cyclopids:** *Mesocyclops brasilianus* Kiefer, 1933 and *Thermocyclops decipiens* Kiefer, 1927. Comments: This set of records resulted from an ecological investigation of epibiotic populations of an unidentified species of *Epistylis* in a reservoir in northwestern Venezuela. No description of the epibiont was given, and therefore, there is no way of being certain that only one species of *Epistylis* was involved although this seems to be implied by the authors.

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2. This species has had a complicated and confusing nomenclatural history, having been known under several names in four different genera until its identity was clarified by Foissner *et al.* (1999). For the sake of clarity, records are listed under the names that were used in the original sources. Junior synonyms of *E. pygmaeum* for which records on cyclopoid copepods have been published are the following: *Carchesium pygmaeum* Ehrenberg, 1838; *Scyphidia pyriformis* (Müller, 1773) sensu Perty (1852); *Rhabdostyla ovum* Kent, 1881; and *Epistylis ovum* n. comb in Stiller (1931).

The following species form relatively large, tall colonies:

- ***Epistylis anastatica***[3] **(Linnaeus, 1767); records on substrates other than cyclopoid copepods (as *E. anastatica*):** widespread on small, planktonic crustaceans, including unidentified copepods (Lake Victoria, Tanzania; Daday, 1910), and aquatic plants (see Keiser 1921 for sources from the older literature); **(as *E. nympharum*):** unidentified dipteran larva (type host), larvae of mosquitoes, midges, mayflies and caddisflies, aquatic beetles, aquatic snails, calanoid copepods (*Eudiaptomus gracilis* [G.O.Sars, 1862]); lernaeopodid copepods (*Achtheres percarum* Nordmann, 1832; *Tracheliastes maculatus* Kollar, 1835; order Siphonostomatoida), cladocerans, ostracods, isopods, amphipods (see Keiser 1921 and Matthes, 1950 for sources of records); *Dolops ranarum* (Stuhlmann, 1891) (branchiuran), South Africa (Van As & Viljoen, 1984); *Lepidurus apus* (Linnaeus, 1758) (branchiopod), Austria (Foissner *et al.*, 1999); **records on cyclopids (as *E. anastatica*):** unidentified cyclopids, England (Green, 1974); **(as *E. lacustris*):** *Megacyclops viridis*, Germany (Hofer, 1899; Nenninger, 1948); *Cyclops* spp., Switzerland (Mermod, 1914); *Cyclops strenuus*, Switzerland (Heuscher, 1917); *Eucyclops serratulus*, *M. viridis*, *Paracyclops fimbriatus*, Switzerland (Monard, 1919); *M. viridis, E. serratulus, Macrocyclops fuscus, Macrocyclops albidus, Mesocyclops leuckarti;* Switzerland (Keiser, 1921); *Cyclops* sp., China (Wang & Nie, 1933); *Cyclops* sp., Italy (Canella, 1954); *Eucyclops agilis* (Koch, 1838), *M. albidus*, Macedonia (Green, 1960); *Cyclops* sp., Austria (Foissner & Schiffman, 1975); *Cyclops* sp., Slovakia (Stloukal, 1999); *Cyclops* sp., Brazil, Mato Grosso do Sul, Corumbá (Daday, 1905); **(as *E. nympharum*):** *P. fimbriatus*, Switzerland (Monard, 1919); *M. albidus*, Switzerland (Keiser 1921); *Cyclops* sp. (Stiller, 1942); *E. serratulus*, Germany (Sommer, 1951); *E. serrulatus*, Slovakia (Stloukal, 1999).
- ***Epistylis digitalis* (Linnaeus, 1758); records on substrates other than cyclopoid copepods:** dipteran larvae (type host), water mites, aquatic plants (*Ceratophyllum*, *Lemna*); Denmark, Germany, England, Switzerland (see citations in Matthes, 1950 for sources of records); **records on cyclopids:** *Cyclops quadricornis*, Germany (Ehrenberg, 1830); *C. quadricornis*, Switzerland (Perty, 1852); *C. quadricornis*, England (Pritchard, 1852); *C. quadricornis*, Germany (Stein, 1854); *Cyclops* spp., Hungary (Francé, 1897); *Cyclops* sp., Switzerland (Roux, 1901); *Eucyclops serratulus*, Switzerland (Monard, 1919); *Diacyclops bisetosus*, *E. serratulus*, *Macrocyclops fuscus*, Switzerland (Keiser, 1921); *Megacyclops viridis*, Germany (Nenninger, 1948); *E. serratulus*, Germany (Sommer, 1949); *Acanthocyclops vernalis*, *Diacyclops bicuspidatus*, Germany (Matthes, 1950); *Eucyclops agilis*, Macedonia (Green, 1960).
- ***Epistylis niagarae* Kellicott, 1883; records on substrates other than cyclopoid copepods:** widespread on astacid crayfish in the following genera (and possibly others): *Cambarus* Erichson, 1846, *Cambarellus* Ortmann, 1905, *Astacus* Fabricius, 1775 (Matthes & Guhl, 1973); **records on cyclopids:** *Eucyclops serrulatus*, Colorado, USA (Willey & Threlkeld, 1993); *Cyclops vicinus*, Turkey (Saler & Dörüc, 2008); *Mesocyclops aspericornis* (Daday, 1906), India (Rajabunizal & Ramanibai, 2011). Comments: All records of *E. niagarae* on cyclopoid copepods are misidentifications. Willey and Threlkeld (1993) do not give any features of the species that they observed, and the SEM micrograph that they present is grossly insufficient as evidence. Moreover, one of the few things that can be seen from their SEM views is that the colony is much too small and short to be *E. niagarae*; consequently, this record is listed as *Epistylis* sp. in Table 3. The record of *E. niagarae* by Saler and Dörücü (2008) on *C. vicinus* in Turkey is an obvious misidentification—the epibiont is a small species that does not form colonies and, thus, may be a member of the genus *Rhabdostyla*. Their only photomicrographs show contracted, featureless cells with no visible stalk, which means that they cannot even be identified with confidence as members of *Rhabdostyla* Kent, 1881. The species observed by Rajabunizal & Ramanibai (2011) on *M. aspericornis* from a lake in Chennai, India is shown and described as having a contractile myoneme that runs continuously through the stalk, a feature that marks it as a member of the genus *Zoothamnium*, certainly not *Epistylis*.
- ***Epistylis plicatilis* Ehrenberg, 1830; records on substrates other than cyclopoid copepods:** reported from a wide variety of aquatic substrates, including aquatic plants, algae, crustaceans, insects and insect larvae, snails, and inanimate objects; **records on cyclopids:** *Cyclops* sp., Switzerland (Roux, 1901); *Mesocyclops leuckarti*,

3. *Epistylis lacustris* Imhof, 1884 and *E. nympharum* Engelmann, 1862 are subjective junior synonyms of *E. anastatica* (Foissner *et al.*, 1992, 1999). For the sake of clarity, records are listed under the names that were used in the original sources

Kenya, Tanzania Daday, 1910); *Cyclops* sp., Switzerland (André, 1912); *Cyclops* sp., Germany (Haempel, 1918); *Acanthocyclops vernalis, Cyclops strenuus, Eucyclops serratulus*, Switzerland (Keiser, 1921); *A. vernalis*, *Diacyclops bicuspidatus*, *Eucyclops agilis*, USA (Henebry & Ridgeway, 1979). Comments: The records in Henebry & Ridgeway (1979) from southern Illinois, USA, are doubtful. Their photomicrograph of colonies of *E. plicatilis* on copepods shows tightly packed colonies that are ~200–300 µm tall and are thus not typical of *E. plicatilis*, which can form colonies up to 4000 µm tall (Foissner *et al.*, 1999). Furthermore, the few zooids that are visible in their figure do not appear to have the elongate, slender shape that is typical of *E. plicatilis*. Instead, their species most closely resembles *E. pygmaeum*.

The following species of *Epistylis* have been reported from lernaeid cyclopoids parasitic on freshwater fishes in South Africa by Van As & Viljoen (1984):

- ***Epistylis branchiophila* Perty, 1852; records on substrates other than cyclopoid copepods:** larvae of caddisflies (type host); **record on lernaeid:** *Lernaea cyprinacea* Linnaeus, 1758 from *Oreochromis mossambicus* (Peters, 1852). Comments: This record is certainly a misidentification. The species described by Van As & Viljoen (1984) and depicted in their figures is distinctly different from *E. branchiophila* as described and depicted in Perty (1852). It is tall and arborescent in overall form, with a long primary stalk, many zooids on symmetrically dichotomous branches, and zooids that are cylindroid to ovoid. All of these characteristics differ markedly from the description of *E. branchiophila* in Perty (1852). Moreover, Van As and Viljoen (1984) list another species found on caddisflies, *E. formosa* Nenninger, 1948, as a synonym of *E. branchiophila*. This is highly unlikely because *E. formosa* has small colonies with symmetrically dichotomous branching, its zooid is ovoid, and contraction of the zooid causes it to have a pair of circumferential folds that encircle the posterior third of the body and appear to be unique to this species. In the final analysis, the species identified as *E. branchiophila* by Van As and Viljoen (1984) cannot be identified with confidence, and it is likely that it represents a species new to science.
- ***Epistylis cyprinaceae* Van As & Viljoen 1984; records on substrates other than cyclopoid copepods:** none; **records on lernaeid:** *Lernaea cyprinacea* from *O. mossambicus* and *Labeo congoro* Peters, 1852 (under the synonymous name *L. rubropunctatus* Gilchrist & Thompson, 1913). Comments: The consistent presence of macrozooids in this species is unusual among members of *Epistylis*. Only one other species, *Epistylis ophidiodea* Kellicott, 1884, is described as being dimorphic, and the occurrence of different sizes of zooids in a colony of *E. galea* Ehrenberg, 1831 appears to have been incidental and could be attributed to zooids being in different stages of the cell cycle (Matthes & Scheubel 1970). Macrozooids are present in the colonies of *Systylis hoffi* Bresslau, 1919 (family Epistylididae) and some members of the genus *Zoothamnium* (family Zoothamniidae), where they are specialized for reproduction of the colony (i.e., macrozooids divide to form microconjugants and motile telotrochs for dispersal, and microzooids divide to add vegetative individuals during development of the colony). Van As and Viljoen (1984) did not observe whether the macrozooids of *E. cyprinaceae* were specialized for reproduction of the colony.
- ***Epistylis epibarnimiana* Van As & Viljoen 1984; records on substrates other than cyclopoid copepods:** none; **record on lernaeid:** *Lernaea barnimiana* (Hartmann, 1865) from *Labeo capensis* (Smith, 1841).
- ***Epistylis magna* Van As & Viljoen 1984; records on substrates other than cyclopoid copepods:** none; **record on lernaeid:** *Lernaea cyprinacea* from *O. mossambicus*.

Summary of records of *Epistylis* spp. on cyclopoid copepods. Eleven species of *Epistylis* have been reported as epibionts of cyclopid hosts and four species have been reported as epibionts of lernaeid hosts (Table 3). All of the records of *E. niagarae* on cyclopids are misidentifications; therefore, it should be removed from the list. The record of *E. branchiophila* on *Lernaea cyprinacea* (Van As & Viljoen, 1984) is a misidentification and may represent an undescribed species of *Epistylis*; consequently, it is listed as *Epistylis* sp. in Table 3.

Twenty species of cyclopids and two species of lernaeids have been recorded as hosts of epibiotic species of *Epistylis* (Table 3). Records of *Epistylis niagarae* on *C. vicinus* (Saler & Dörüc, 2008) and *Mesocyclops aspericornis* (Rajabunizal & Ramanibai, 2011) are misidentifications that apparently do not represent species of *Epistylis*; consequently, these records are omitted from Table 3.

Documentation of occurrences of epizoic peritrichs on microcrustaceans and other hosts. Many of the

records of *Epistylis* spp. and members of other genera of peritrichs as epibionts of crustaceans are not documented by figures, descriptions, or voucher material (Foissner *et al.*, 1999). Typically, these records appear as items in lists or tables of papers on aquatic ecology. While useful in a general way for basic description of community composition or structure, such records are of extremely limited use to future investigators.

At the very least, authors should provide some means of verifying their identification of epibionts, such as supplementary descriptions, high-quality photomicrographs of living specimens, or voucher specimens of infested hosts fixed and preserved in 95% alcohol and deposited in a permanently curated museum collection. The latter would be especially useful because they would constitute a source of DNA for molecular investigations. In the present study, we attempted to obtain a partial sequence of the gene coding for small-subunit rRNA to enable a comparison with samples of *E. anastatica* that were found on copepods in the U.S (data from these samples will be included in a planned paper on phylogenetics of epizoic species of *Epistylis* and, therefore, are not given here). Unfortunately, efforts to amplify the target sequence from DNA extracted from colonies of *E. anastatica* collected in India using ciliate-specific and peritrich-specific primer sets failed, possibly because initial fixation of the sample was not suitable for preservation of DNA.

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